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The involvement of subcortical grey matter in verbal semantic comprehension: A systematic review and meta-analysis of fMRI and PET studies

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ABSTRACT

Semantic processing is a fundamental aspect in human communication. The cortical organization of semantic processing has been exhaustively described, in contrast to inconsistent results on the function of subcortical grey matter structures. Hence, this manuscript reports a systematic review and meta-analysis on the subcortical involvement in verbal semantic comprehension in healthy individuals. The 50 included studies indicate specific contributions by the cerebellum, thalamus and caudate nucleus respectively. In particular, the right posterior cerebellum is proposed to be involved in a semantic executive system and in adequate decision-making. The left thalamus, regulated by the caudate nucleus, might function as a subcortical hub, controlling the access and integration of cortically organized semantic features. Furthermore, a contribution of the cerebellum, thalamus and caudate nucleus in semantic prediction generation and evaluation at sentence level is preliminarily suggested. More research is required to gain insights into the role of the putamen, globus pallidus and subthalamic nucleus.

1. Introduction

Semantic processing, or the ability to store and access the knowledge we acquired through life experiences, is a fundamental aspect of human communication (Binder, Desai, Graves, & Conant, 2009). The term “semantics” was first introduced by Michel Bréal as “science of the meanings of words and of the changes in their meaning” (Bréal, 1883). For years, neuroscientists have been interested in the neural correlates of verbal semantic processing, especially at the cortical level. Concerning semantic word comprehension, several neurocognitive theories propose that meaning is grounded in the perception, action and affective systems of the brain (Binder & Desai, 2011; Garagnani & Pulvermüller, 2016; Pulvermüller & Fadiga, 2010). For example, the hub and spoke model suggests the existence of modality-specific association areas (spokes), storing sensorimotor and affective information, and a higher-level convergence area (hub), integrating the modality-specific information to form supramodal representations (Binder & Desai,

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2011; Patterson, Nestor, & Rogers, 2007; Ralph, Jefferies, Patterson, & Rogers, 2017; Rogers et al., 2004). These supra-modal representations capture conceptual similarities that define semantic categories (Binder & Desai, 2011; Patterson et al., 2007) (see Huth, de Heer, Griffiths, Theunissen, and Gallant (2016) for a cortical atlas of twelve semantic categories by means of voxel-wise modeled fMRI-data). Neuro-anatomically, the anterior temporal lobe of the language dominant hemisphere has been identified as the higher-level convergence area in multiple studies (Patterson et al., 2007; Ralph, Sage, Jones, & Mayberry, 2010; Visser & Ralph, 2011), although Binder and Desai (2011) argue that there are multiple critical semantic hubs in the lateral and ventral temporal cortex and in the inferior parietal lobe. Besides the organization of semantic knowledge, control processes are needed in order to retrieve and select the appropriate information based on contextual demands. These processes have been linked to the anterior and posterior parts of the inferior frontal cortex (Devlin, Matthews, & Rushworth, 2003; Gold, Balota, Kirchhoff, & Buckner, 2005; Thompson-Schill, Bedny, & Goldberg, 2005; Whitney, Kirk, O'sullivan, Lambon Ralph, & Jefferies, 2010). Badre and colleagues specified that controlled semantic retrieval relies on the anterior IFG (BA 47), whereas the mid-posterior IFG (BA45) is critical for semantic selection processes (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2007).

In semantic comprehension at sentence level, similar interactions between frontal and temporo-parietal structures have been documented. A reference can be made to the dual-route model of Hickok and Poeppel (Hickok & Poeppel, 2007), who propose two ventral and two parallel dorsal pathways (Friederici, 2012; Friederici & Gierhan, 2013) in which a bi-directional flow of information (bottom-up/top-down) is suggested (Friederici & Gierhan, 2013). This flow of information is provided by specific white matter fiber bundles, connecting frontal, temporal, parietal and occipital areas (see Catani and de Schotten (2012) for anatomical details). Especially the ventral inferior fronto-occipital fasciculus (IFOF), connecting inferior frontal and superior temporal cortices, has been consistently linked to support semantic organization and control (Almairac, Herbet, Moritz-Gasser, de Champfleur, & Duffau, 2015; Berwick, Friederici, Chomsky, & Bolhuis, 2013). However, a contribution of the dorsal arcuate fasciculus has also been reported (Leclercq et al., 2010; Rilling et al., 2008; Welcome & Joanisse, 2014).

At the subcortical level, knowledge on the neural correlates of language processing is less extensive. Nevertheless, the importance of subcortical structures has already been pointed out in early clinical studies by Pierre Marie and his student Moutier in 1906 (Marie, 1906). Their descriptions of subcortical aphasias formed the basis of further research on subcortical involvement in language processing. Focusing on semantics, comprehension disorders have been extensively reported in patients with subcortical lesions (Demonet, 1997). Moreover, semantic paraphasias are one of the most prominent features of thalamic aphasias (Crosson et al., 1986; Kuljic-Obradovic, 2003). Additional evidence that subcortical structures are key components of the neural semantic networks is provided by neurodegenerative disorders, such as Parkinson's Disease (PD). Both lexical-semantic deficits and a semantic processing delay have been reported in studies with nondemented PD patients (Angwin et al., 2009; Arnott et al., 2010; Arnott, Chenery, Murdoch, & Silburn, 2001; Kemmerer, Miller, Macpherson, Huber, & Tranel, 2013).

Based on the correlations between language disorders and brain lesions, several models have proposed subcortical functions to mediate semantic processing. In the original Selective Engagement model, Nadeau and Crosson proposed a bi-directional interaction between the thalamus (the nucleus reticularis and the centromedian nucleus) and the frontal cortex, responsible for a temporary engagement of the cortical areas representing specific semantic features ("modality-specific spokes"), while maintaining other areas in a state of relative disengagement (Crosson, 1985; Nadeau & Crosson, 1997). Hence, the thalamus is considered to gate the semantic information flow between frontal and temporo-parietal areas by monitoring their activity. This model heavily influenced contemporary thinking and provided the basis for more recent models in which anatomical modifications have been implemented. For example, Kraut, Calhoun, Pitcock, Cusick, and Hart (2003a, 2003b) described the Neural Hybrid Model of Semantic Memory in which they suggested a role of the dorsomedial and pulvinar nucleus in semantic feature search and binding processes respectively. Moreover, the Selective Engagement model has been extended by considering the functional role of the basal ganglia. Stocco, Lebiere, and Anderson (2010) described their role as "determining the state of cortical regions". Relying on the neuro-anatomical cortico-striato-thalamo-cortical loops (Alexander, DeLong, & Strick, 1986; Jahanshahi, Obeso, Rothwell, & Obeso, 2015; Murdoch, 2009), such a modulation of cortical semantic areas must be mediated through the thalamus. Indeed, several authors reported a fronto-striato-thalamic circuit responsible for the activation of (cortically organized) semantic features or concepts with a high utility in a certain linguistic context (Kraut et al., 2003a, 2003b; Scimeca & Badre, 2012). In this line, Chenery, Angwin, and Copland (2008) suggested that an integrated cortical-striato-thalamic circuit is responsible for the enhancement and suppression of ambiguous word meanings. Moreover, Hart et al. (2013) described a pre-SMA-caudato-thalamic circuit underlying the (de)activation of integrated concepts in semantic memory.

In addition to the involvement of the basal ganglia and thalamus, the role of the cerebellum in language processing has gained scientific interest. Besides the well-established role in motor speech control (Manto et al., 2012; Riecker et al., 2005), cerebellar contributions to cognitive and linguistic processing have become an emergent topic in the neuroscientific literature (Mariën et al., 2014). As the cerebellum is connected with motor, association and paralimbic regions through cerebello-thalamo-cerebral pathways (Voogd & Glickstein, 1998), it could operate as an essential modulator of higher-level cortical functions such as semantic prediction during sentence processing (D'Mello, Turkeltaub, & Stoodley, 2017).

In this manuscript, we present a systematic review of the involvement of subcortical grey matter[2] structures in verbal semantic

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[2] Grey matter refers to the neuronal cell bodies, dendrites, axons and glial cells that are located on the surface of the cerebral cortex, the subcortical nuclei and the cerebellum, and in the spinal cord. In this systematic review, only the subcortical nuclei and the cerebellum (Murdoch, 2009) are considered. A systematic overview of the contribution of subcortical white matter tracts in verbal-semantic comprehension is beyond the scope of this paper.

comprehension. As neuro-anatomic and neurocognitive representation strongly depend on the type of task used during neuroimaging, the following paragraphs provide a short overview of verbal semantic comprehension tasks at word and sentence level. At word level, meaning depends on the semantic relationship among individual words. Two classic tasks to investigate verbal semantic comprehension are word categorization and association. Categorization is fundamental to understand and use the concepts in semantic memory, as this process organizes our knowledge and relates items to other familiar items. At least two types of categorization processes can be distinguished. In *similarity-based categorization*, category membership is determined by the overall similarity to category examples or to prototypes. This process involves a global comparison of the test item with memorized instances of the category, or a comparison with an abstracted prototype representing category members (Medin, Goldstone, & Gentner, 1993). In *rule-based categorization*, specific features must be considered. A test item is evaluated with reference to specific rules representing category membership criteria (Smith, Patalano, & Jonides, 1998; Smith & Sloman, 1994). The latter type of categorization requires multiple executive processes such as working memory, selective attention, inhibitory control and task switching (Grossman et al., 2002). A second task within the research of semantic word comprehension is association, which is dissociable in two major subtypes: (1) compositional association (two items are associated, but retain their individuality – e.g. fork and knife), and (2) noncompositional association (two items become semantically fused – e.g. computer and virus) (Kounios, Smith, Yang, Bachman, & D'Esposito, 2001). An application of the noncompositional type of association is the Semantic Object Retrieval Task (SORT). SORT is a semantic fusion task in which participants push a button if two combined features (e.g. desert and hump), make them think of a third object (e.g. camel) (Kraut et al., 2007). Besides the classical categorization and association tasks, several other tasks have been used to investigate semantic word comprehension (e.g. synonym, ambiguity and reading tasks).

At sentence level, comprehension depends on orthographic/phonological, semantic, (morpho)syntactic and prosodic information (Friederici, 2011). When focusing on semantics, orthographic, phonological, (morpho)syntactical and prosodic demands need to be controlled for. An example of a verbal semantic comprehension paradigm is the comparison of processing semantically implausible sentences with the processing of plausible sentences. When listening or reading, internal models might support comprehension, by using the context of a partially presented sentence in order to predict the upcoming information (Lesage, Morgan, Olson, Meyer, & Miall, 2012). Processing implausible sentences creates a mismatch between what is expected and the actual incoming information and can provide important insights into (sub)cortical functions.

Neuroimaging experiments have fundamentally expanded our knowledge on the neural correlates of verbal semantic comprehension. Nevertheless, a consensus on the precise function of the subcortical grey matter structures is lacking. Therefore, the aim of this systematic review is to investigate the role of the subcortical grey matter structures in verbal semantic comprehension by summarizing the current knowledge. We only included studies with healthy individuals in order to avoid misinterpretations about the role of a specific structure due to neuroplastic changes in patients with subcortical lesions. In healthy participants, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) can be used to visualize subcortical activity. Both imaging techniques are characterized by a high spatial and relatively low temporal resolution. Thus, spatial and dynamic aspects of subcortical activation patterns were analyzed in the available fMRI and PET literature. We hypothesize that the subcortical grey matter structures contribute to semantic processing by fulfilling specific cognitive functions (Marangolo & Piras, 2010).

In particular, we aim to answer the following research questions:

1. What is the role of the subcortical grey matter structures in semantic word comprehension?
2. What is the role of the subcortical grey matter structures in semantic sentence comprehension?

2. Method

A systematic review on the role of subcortical grey matter structures in verbal semantic comprehension was performed. The general approach to identify, select and summarize the evidence in order to answer the research questions is consistent with the methodology described in the Cochrane Handbook for Systematic Reviews of Interventions. The protocol was registered in advance on Prospero (registration number: CRD42017056950).

The following electronic databases were systematically searched to identify studies relevant to this review: Web of Science, Medline (using the PubMed interface), The Cochrane Central Register of Controlled Trials (CENTRAL), and Embase (using the Embase.com interface). The strategies used to search the abovementioned databases are available in Appendix 1. The searches in each database were performed on February 6, 2017 and the references were exported into a reference manager software tool (Endnote) in order to remove the duplicates and to perform a screening by titles and abstracts. One author (E.M.C.) removed all the duplicate records. Subsequently, titles and abstracts identified by the search were screened for relevance to the research questions by two independent reviewers (E.M.C. and C.C.). During this screening, specific eligibility criteria were taken into account (Table 1). After the exclusion of records according to title and abstract, the full-texts of the remaining references were accessed through SFX (UGent-collection). When no full-text was available, attempts were made to contact the authors. Next, the full-texts were screened against the eligibility criteria. Disagreements on the inclusion of articles were resolved by discussion or by involving a third reviewer (M.D.L) until a consensus was reached. After reading the selected articles, all the results were processed in a summary table (available from the first author upon request). In addition, the quality of the selected articles was evaluated with a scoring system including multiple aspects of the introduction, methods, results and discussion section in order to secure the validity of the articles. The aspects could achieve a maximum score of 1 or 2, depending on their relative value. The scoring system was based on the “Quality Assessment Tool for Observational Cohort and Cross-Sectional Studies” of the National Institute of Health (https://www.nhlbi.nih.gov/). The detailed terms and weighted distribution of points for each aspect can be found in Appendix 2.

Table 1
Overview of the eligibility criteria used for the selection of articles in the systematic review.

Eligibility criteria	Inclusion criteria
Population	- Adults (male or female) - Right-handed - No cognitive or psychological disorders - No developmental or genetic disorders - Native language is a Germanic or Romance language
Intervention	- A verbal semantic comprehension task (in the participants' native language) during functional magnetic resonance imaging (fMRI) or positron emission tomography (PET)
Research parameters	- Subcortical activation patterns resulting from the contrasts between a verbal semantic comprehension task and a control task
Publication type	- A1-publication peer-reviewed - Written in English - Prospective study - Group or case study - All publication years included until February 6, 2017

In order to identify consistent regions of subcortical activation, a coordinate-based meta-analysis of functional neuroimaging data was used. More specifically, the meta-analysis was performed using the revised algorithm of the activation likelihood estimation (ALE) approach, implemented in BrainMap GingerALE 2.3.6. (Eickhoff et al., 2009). This method does not treat the activation foci as single points but as Gaussian probability distributions centered at the given coordinates. Convergence of the activated foci is determined by computing ALE-values constructed to reveal the activation probabilities of each voxel. For our meta-analysis, we used the more conservative non-additive ALE-method because it limits the bias of resulting ALE-values as a result of studies reporting multiple foci within close proximity. Also, the non-additive ALE-method results in smaller cluster extents, allowing more precise localization (Turkeltaub et al., 2012). Significance of convergence across studies was determined by a permutation test comparing the ALE-maps against a null distribution determined empirically to model spatial uncertainty (Eickhoff et al., 2009). The analysis was corrected for multiple comparisons by the voxel-level False Discovery Rate pN-method at $q < 0.05$ (Genovese, Lazar, & Nichols, 2002; Laird et al., 2005). Also, a minimum cluster size of $100\,mm^3$ was applied to the final thresholded ALE-map, following Molenberghs, Cunnington, and Mattingley (2012). The significant clusters in the final ALE-map were described according to the Talairach Daemon Data labels included in GingerALE 2.3.6 (Lancaster et al., 2000). In this meta-analysis, we only used the Talairach coordinates (Talairach & Tournoux, 1988) of the activated subcortical foci. Montreal Neurological Institute (MNI) coordinates were converted by using the built-in transformation algorithm in BrainMap GingerALE 2.3.6. The final ALE-maps were exported into the Mango brain visualization software (http://ric.uthscsa.edu/mango/) and overlaid on an anatomical brain template (Colin_tlrc_2 × 2 × 2, distributed by BrainMap GingerALE).

3. Results

3.1. Review characteristics

Study selection process - A flowchart of the identification and selection of the studies is provided in Fig. 1 (Moher, Liberati, Tetzlaff, Altman, & Group, 2009). The literature search in the electronic databases yielded 3337 articles. After removing duplicates and triplicates, 1818 records remained. Screening of titles and abstracts resulted in 155 references. After full-text screening, 104 studies were excluded because the selection criteria were not met and one full-text was lacking. Fifty studies met the inclusion criteria and were included for analysis. Thirty-eight of the included studies investigated semantic comprehension at word level and 11 studies at sentence level. One study described both word and sentence comprehension (McAvoy et al., 2016). Further, 23 studies (25 experiments) on word level comprehension were included in the meta-analysis (*Categorization:* Chee, O'Craven, Bergida, Rosen, & Savoy, 1999; Gold & Buckner, 2002; Harris et al., 2006; Jennings, McIntosh, Kapur, Tulving, & Houle, 1997; Kellenbach, Brett, & Patterson, 2001; Lepage, Habib, Cormier, Houle, & McIntosh, 2000; Mandzia, Black, McAndrews, Grady, & Graham, 2004; Noppeney & Price, 2002; Pilgrim, Fadili, Fletcher, & Tyler, 2002; Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Rossion et al., 2000; Tieleman et al., 2005; Welker, De Jesus, Watson, Machulda, & Jack, 2012; Wirth et al., 2011 – *Compositional association:* Assaf et al., 2006; Fenker et al., 2010; Martins, Simard, & Monchi, 2014; McDermott, Petersen, Watson, & Ojemann, 2003; Mummery, Patterson, Hodges, & Price, 1998; Seghier & Price, 2013; Simard, Monetta, Nagano-Saito, & Monchi, 2013; Weber, Lau, Stillerman, & Kuperberg, 2016; Whatmough, Verret, Fung, & Chertkow, 2004). Due to the low number of studies and to the methodological heterogeneity of comprehension tasks at sentence level, no meta-analysis could be performed.

Quality of evidence of the included studies - Figs. 2 and 3 show the overall quality of the 38 (plus one[3]) studies with results on the subcortical involvement in semantic word comprehension and of the 11 (plus one[1]) studies with results on sentence comprehension. Concerning the *introduction*, the aims of the study or research questions were accurately mentioned in each article. In general, the *method* section was characterized by a good quality, both for the studies on word comprehension (75.5%) as well as on

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[3] McAvoy et al. (2016) reported results on both verbal semantic word and sentence comprehension.

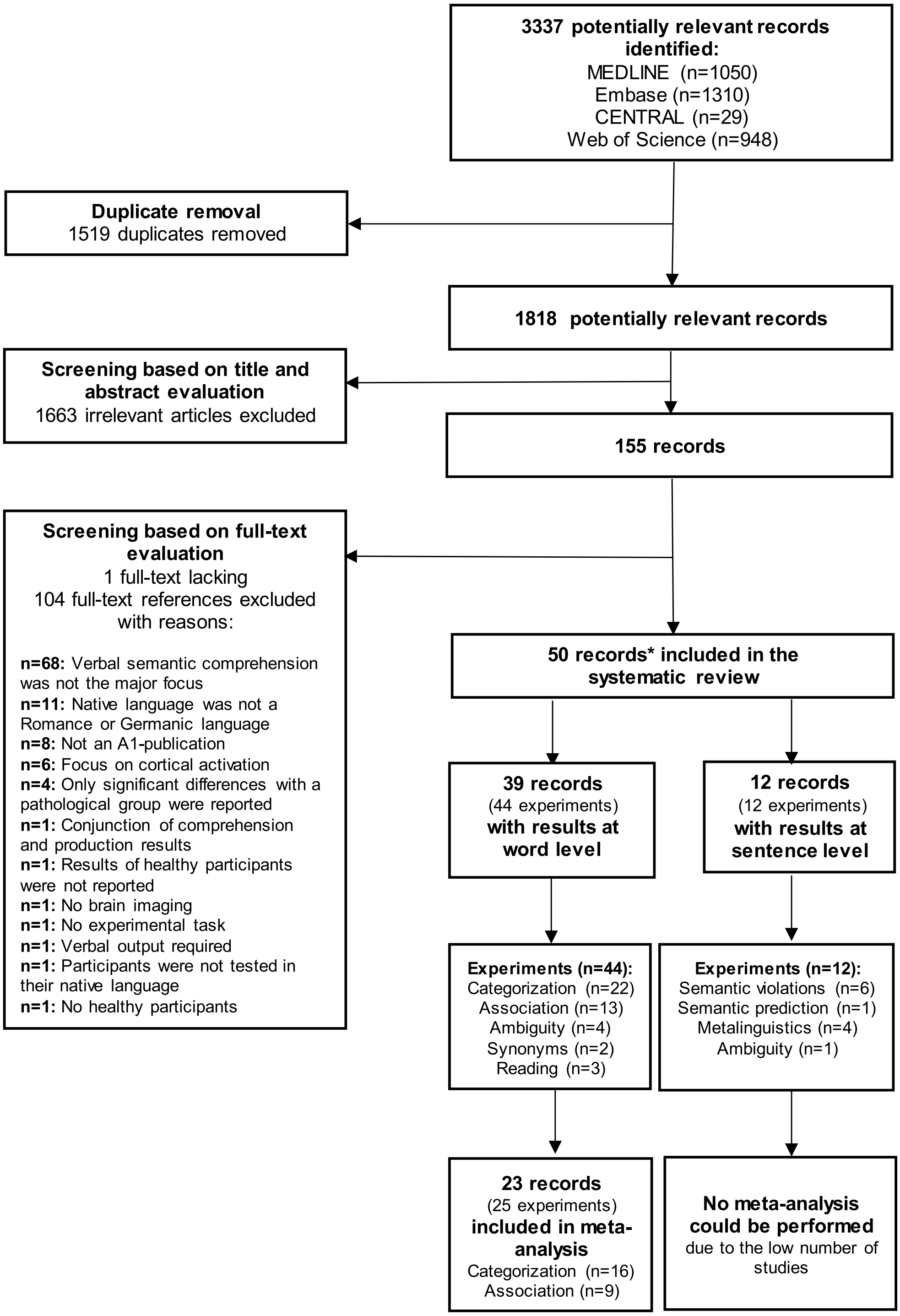
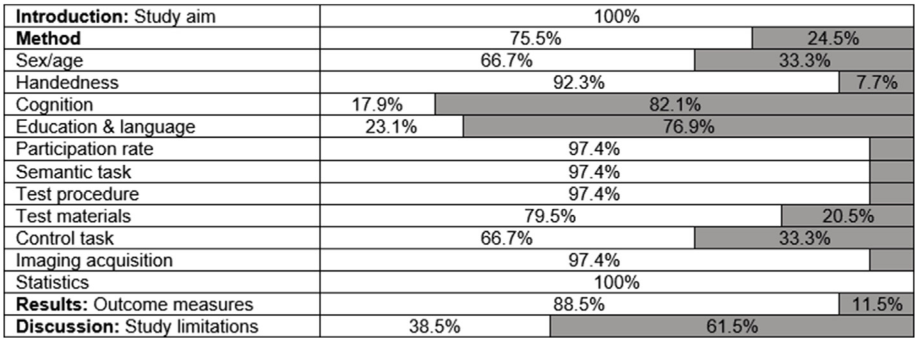


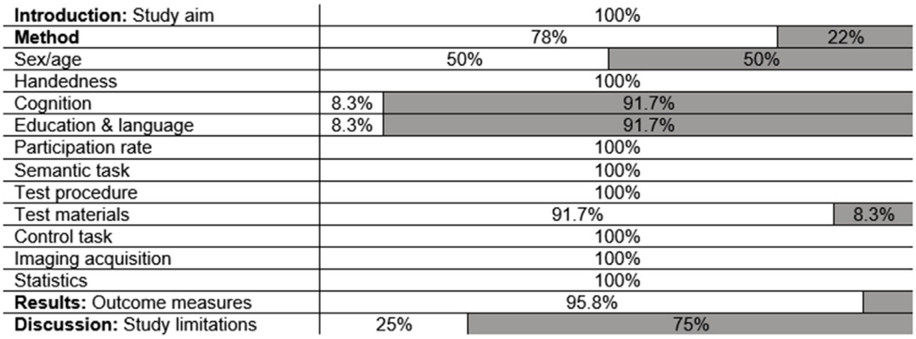
Fig. 1. Flowchart of the identification and selection of studies (based on the PRISMA flowchart – adapted from Moher et al. (2009)) - * In one study, the neural correlates of both semantic word and sentence comprehension were reported.

sentence comprehension (78%). However, certain methodological limitations should be considered when interpreting the study results. The most notable limitation concerning the population was the limited use of a standardized test to assure normal cognition. Only 7 studies at word level (17.9%) and one at sentence level (8.3%) made use of such a test (e.g. Mini-Mental State Examination, Montreal Cognitive Assessment). Further, only 9 studies at word level (23.1%) and one at sentence level (8.3%) reported the educational level of the subjects. Regarding the semantic task, a clear description and argumentation of the selected experiment and procedure was provided in most of the studies. Nevertheless, 15 studies at word level (33.3%) used a control task in which the



Introduction: Study aim	100%	
Method	75.5%	24.5%
Sex/age	66.7%	33.3%
Handedness	92.3%	7.7%
Cognition	17.9%	82.1%
Education & language	23.1%	76.9%
Participation rate	97.4%	
Semantic task	97.4%	
Test procedure	97.4%	
Test materials	79.5%	20.5%
Control task	66.7%	33.3%
Imaging acquisition	97.4%	
Statistics	100%	
Results: Outcome measures	88.5%	11.5%
Discussion: Study limitations	38.5%	61.5%

Fig. 2. Quality of the introduction, method, results and discussion section of the 39 studies with results on the subcortical involvement in semantic comprehension at **word level** (white = high quality, grey = low quality).
We refer to Appendix 2 for the detailed terms and weighted distribution of points for each row header.



Introduction: Study aim	100%	
Method	78%	22%
Sex/age	50%	50%
Handedness	100%	
Cognition	8.3%	91.7%
Education & language	8.3%	91.7%
Participation rate	100%	
Semantic task	100%	
Test procedure	100%	
Test materials	91.7%	8.3%
Control task	100%	
Imaging acquisition	100%	
Statistics	100%	
Results: Outcome measures	95.8%	
Discussion: Study limitations	25%	75%

Fig. 3. Quality of the introduction, method, results and discussion section of the 12 studies with results on the subcortical involvement in semantic comprehension at **sentence level** (white = high quality, grey = low quality). We refer to Appendix 2 for the detailed terms and weighted distribution of points for each row header.

phonological or orthographic demands were not comparable with the phonological or orthographic demands in the semantic task. The *results* section had a good quality, both for the studies on word comprehension (88.5%) as well as on sentence comprehension (95.8%) with a precise description of imaging results, supplemented with clear figures and tables. Last, the *discussion* section had a rather low quality due to the scarce reporting of study limitations (word level: 38.5% - sentence level: 25%).

In the sections below, the results on the subcortical involvement in each type of semantic comprehension task are reported. First, we describe the results of the studies included in a meta-analysis. Second, we provide the results of the remaining articles (not included in an ALE-analysis) in a narrative synthesis.

3.2. Semantic word comprehension

3.2.1. Meta-analysis (ALE)

Twenty studies (22 experiments) reported the neural correlates of word *categorization* tasks. Specific details on the content of the categorization tasks can be found in Table 2. Fourteen studies, 16 experiments (one similarity-based, fifteen rule-based), 244 subjects and 29 foci were included in the ALE-analysis. The meta-analysis revealed 2 above-chance significant clusters located in the *right posterior cerebellum* (Table 3, Fig. 4). Four studies with lacking coordinates could not be included in the ALE-analysis, but right cerebellar activity was reported both in the rule- and similarity-based categorization tasks (Fulbright, et al., 1999; Halai, Welbourne, Embleton, & Parkes, 2014; Kennedy et al., 2015; Whyte et al., 2006). In 2 studies, no subcortical activation was reported (Grossman et al., 2003; Ragland et al., 2005).

Within the 13 *association* tasks, a distinction was made between compositional (n = 9) and noncompositional tasks (n = 4). The 9 articles reporting a compositional association task were included in the ALE-analysis, which was reflected by 214 subjects and 35 foci. Two above-chance significant clusters were found, namely the *left dorsomedial thalamus* and *right caudate nucleus* (Table 4, Fig. 5).

3.2.2. Remaining articles

In the remaining studies, the neural correlates of noncompositional association (n = 4), ambiguity processing (n = 4), synonym judgment (n = 2) and reading (n = 3) were reported. Results are summarized in Table 5. In 4 studies a *noncompositional association* task was used, more specifically a SORT-task. The SORT-task has been extensively used by Kraut and colleagues. In their studies, object recall-pairs (words) revealed significant activation in the *left dorsal thalamus*, which was not visible for the feature word pairs

Table 2
Content overview of the 20 studies (22 experiments) in which the neural correlates of a **semantic word categorization** task were described.

References	Details on the categorization task			
		Type of categorization task		
	Input mode	Rule-based	Similarity-based	Specific content
Studies included in the meta-analysis (n = 14)				
1. Chee et al. (1999) [a]	Auditory & Orthographic	x		Abstract/concrete
2. Noppeney and Price, (2002)	Auditory	x		Loud/silent
3. Mandzia et al. (2004)	Picture	x		Natural/man-made
4. Rossion et al. (2000)	Picture	x		Small/large
5. Harris et al. (2006)	Orthographic	x		Positive/negative
6. Jennings et al., (1997)	Orthographic	x		Living/non-living
7. Roskies et al. (2001)	Orthographic	x		"Is the bottom word a category member of the upper word?"
8. Welker et al. (2012)	Orthographic	x		"Is the bottom word a category member of the upper word?"
9. Tieleman et al. (2005) [a]	Orthographic	x		Animal/object (a) fixed-paced (b) self-paced
10. Wirth et al. (2011)	Orthographic	x		Living/non-living
11. Gold and Buckner, (2002)	Orthographic	x		Abstract/concrete
12. Lepage et al. (2000)	Orthographic	x		"Is the bottom word a category member of the upper word?"
13. Pilgrim et al. (2002)	Orthographic		x	"Does the target word belong to the same category as the previous cue words?"
14. Kellenbach et al. (2001)	Orthographic	x		Colored/noisy/small
Studies not included in the meta-analysis due to lacking coordinates (n = 4)				
15. Fulbright et al., (1999)	Orthographic		x	"Do the word pairs belong to the same category?"
16. Kennedy et al. (2015)	Orthographic	x		Living/non-living
17. Whyte et al. (2006)	Orthographic	x		Living/non-living
18. Halai et al. (2014)	Orthographic		x	"Does the target word belong to the same category as the previous cue words?"
Studies in which no subcortical activity was reported (n = 2)				
19. Ragland et al. (2005)	Orthographic	x		Abstract/concrete
20. Grossman et al. (2003)	Orthographic	x		Pleasant/unpleasant

[a] Chee et al. (1999) and Tieleman et al. (2005) reported on two experiments.

Table 3
Significant clusters (FDR $q < 0.05$) revealed by the ALE-analysis of 14 studies (16 experiments) using a **semantic categorization** task at **word level**.

Cluster	Activation focus				Anatomical Region	Cluster size (mm^3)
	x	y	z	Hemisphere		
1	15.7	−85.6	−30.7	Right	Posterior Lobe Cerebellum - Tuber	176
2	15.9	−68.1	−34.9	Right	Posterior Lobe Cerebellum - Uvula	144

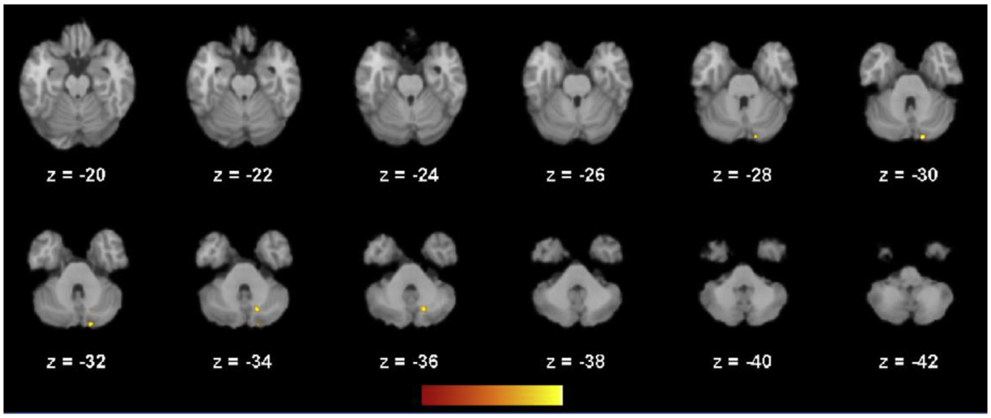


Fig. 4. Axial view of the ALE-map representing the reliably activated clusters at FDR $q < 0.05$ in the *right posterior cerebellum* during semantic word categorization tasks, superimposed on a brain template using Mango.

Table 4

Significant clusters (FDR q $<$ 0.05) revealed by the ALE-analysis of 9 studies (9 experiments) using a **compositional association** task at **word level.**

Cluster	Activation focus			Hemisphere	Anatomical Region	Cluster size (mm^3)
	x	y	z			
1	10.9	8.2	4.7	Right	Caudate nucleus	168
2	−5.2	−12.9	11.5	Left	Thalamus (dorsomedial)	152

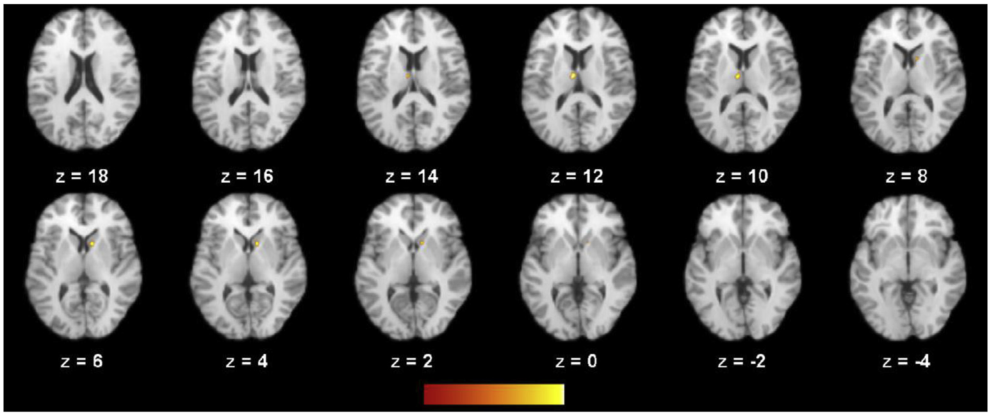


Fig. 5. Axial view of the ALE-map representing the reliably activated clusters at FDR q $<$ 0.05 in the *left thalamus* and *right caudate nucleus* during compositional word association tasks, superimposed on a brain template using Mango.

that did not activate a third object (Kraut et al., 2002a). When using word-picture pairs, object recall-pairs resulted in *bilateral thalamic and caudate activation* (Kraut et al., 2002b). Furthermore, a refinement of their results in Kraut et al. (2002a) revealed two different loci of signal changes in the left thalamus, namely the dorsomedial and pulvinar nucleus. These nuclei exhibited differences in times of onset, peak and return to baseline of signal changes, with the pulvinar nucleus showing the slowest transients of all the examined regions (Kraut et al., 2003a, 2003b). Similar results were reported by Assaf et al. (2006), namely significantly more activation during the object recall events (words) in the *left thalamus* and *right caudate nucleus*. In summary, especially the left thalamus and bilateral caudate nucleus contribute to noncompositional association processing.

Further, studies on the neural correlates of *ambiguous word processing* revealed the involvement of the right cerebellum, left thalamus and bilateral caudate nucleus. Bedny, McGill, and Thompson-Schill (2008) contrasted association conditions in which words referred to the same or different meanings of the ambiguous word (e.g. summer-fan, ceiling-fan versus admirer-fan, ceiling-fan). The whole-brain analyses revealed significant activation in the *right cerebellum*. In addition, *left thalamic* and *bilateral caudate* activation was reported in the studies of Ketteler and colleagues (Ketteler, Kastrau, Vohn, & Huber, 2008a, 2008b; S. Ketteler et al., 2014) in which the subjects needed to press a button when both words, presented at the top of a screen, were related to the target homonym (characterized by a dominant and subordinate meaning), presented at the bottom of the screen. Contrastingly, Kennedy et al. (2015) reported no subcortical activation during the categorization of ambiguous words as either living or non-living.

In 2 studies, the neural correlates of *synonym judgment* tasks were investigated (McAvoy et al., 2016; Roskies et al., 2001). The authors of both studies described an increase of *right posterior cerebellar* activation during the synonym judgment task compared to a control task. In McAvoy et al. (2016), the cerebellar response was larger for abstract than for sensory words. Roskies et al. (2001) also reported activation of the *left putamen* and *the left globus pallidus*.

Finally, the subcortico(cortical) circuits activated during the silent *reading* of category-specific words were investigated in three of the included studies. To explore the brain basis of gustatory semantic links, participants silently read words of which the meaning is primarily related to taste (e.g. salt, bitter, honey). Compared to reading control words, significant activation was measured in the *left thalamus, substantia nigra* and *subthalamic nucleus* (Barrós-Loscertales et al., 2012). In contrast, reading words with an odor-related meaning (e.g. cinnamon, lavender, fetid) was reflected by activation of the *bilateral cerebellum, right putamen, left thalamus* and *left caudate nucleus* (González et al., 2006). Moreover, reading tool words (e.g. hammer, knife, bucksaw) activated the *right cerebellum* and the *left putamen* (Carota, Moseley, & Pulvermüller, 2012).

3.3. Semantic sentence comprehension

Due to the small number of studies (n = 12) and the methodological differences between study experiments on sentence level, no meta-analysis could be performed. Therefore, the results were narratively synthesized. An overview of the results can be found in

Table 5
Overview of the subcortical activation patterns in the 13 remaining studies in which the neural correlates of **semantic word comprehension** were reported.

References	Task content	Task condition	Subcortical activation	
			Hemisphere	Subcortical structures
a) Noncompositional association (n = 4)				
Assaf et al. (2006)	SORT (words)	Correct object recall > no-recall	L	Thalamus
			R	Caudate nucleus
Kraut et al. (2002a)	SORT (words)	Correct object recall > no-recall	L	Dorsal thalamus
Kraut et al. (2003a, 2003b)	SORT (words)	Correct object recall > no-recall	L	Dorsomedial thalamus Pulvinar thalamus (slowest transients of signal changes)
Kraut et al. (2002b)	SORT (words-pictures)	Correct object recall > no-recall	L/R	Dorsomedial thalamus
			L/R	Caudate nucleus
b) Ambiguity task (n = 4)				
Bedny et al. (2008)	Meaning relatedness judgment of word pairs containing an ambiguous word	Consistent: 1st and 2nd word pair referring to the same meaning of the ambiguous word	-	-
		Inconsistent: 1st and 2nd pair referring to a different meaning of the ambiguous word	R	Cerebellum
Ketteler et al. (2014)	Meaning relatedness judgment of word pairs containing an ambiguous word	Homonym condition: both dominant and subordinate meaning related to target homonym	L/R	Caudate nucleus
		Dominant-distractor condition	L	Caudate nucleus
Ketteler et al. (2008a, 2008b)	See Ketteler et al. (2014)	Homonym condition: both dominant and subordinate meaning related to target homonym	L	Dorsomedial thalamus
			L	Pulvinar thalamus
		Dominant-distractor condition	R	Caudate nucleus
Kennedy et al. (2015)	Categorization task (living/non-living)	Ambiguous > unambiguous	-	-
c) Synonym judgment task (n = 2)				
McAvoy et al. (2016)	Synonym judgment	General	R	Cerebellum (posterior)
		Abstract words > concrete words	R	Cerebellum (posterior/lateral inferior)
Roskies et al. (2001)	Synonym judgment	Synonym judgment > rhyme judgment	R	Cerebellum (medial/posterior)
			L	Globus pallidus
			L	Putamen
d) Reading task (n = 3)				
Barrós-Loscertales et al. (2012)	Silent reading	Gustatory words > non-gustatory words	L	Thalamus
			L	Substantia nigra
			L	Subthalamic nucleus
González et al. (2006)	Silent reading	Odor related words > non-odor related words	L/R	Cerebellum
			R	Putamen
			L	Thalamus
			L	Caudate nucleus
Carota et al. (2012)	Silent reading	Tool words > baseline (hashmarks)	R	Cerebellum
			L	Putamen

*SORT = Semantic Object Retrieval Task.

Table 6.

In 6 studies, a *semantic violation* paradigm was used in which the neural correlates of processing semantically plausible and implausible sentences were compared. Participants had to indicate their plausibility judgment by a button response or just attentively listen to or read the sentences. In two studies, no subcortical activation was found (Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Rothermich & Kotz, 2013). In McAvoy et al. (2016), the *right posterior cerebellum* distinguished between plausible and implausible sentences. More specifically, right cerebellar activity increased when listening to implausible sentences. This finding was confirmed in the study of Moberget, Gullesen, Andersson, Ivry, and Endestad (2014) as implausible endings revealed greater activation across an extensive region in the *posterior cerebellum, bilaterally*. In Ye, Doñamayor, and Münte (2014), the semantic incongruity of sentence endings revealed a modulation of the *left caudate nucleus*, namely a stronger connection with the left supplementary motor area (SMA) and right thalamus. However, caudate activation was restricted to the right hemisphere in Kuperberg, Sitnikova, and Lakshmanan (2008). Summarized, these four studies showed the importance of the right (posterior) cerebellum and the left and right caudate nucleus in the processing of semantic violations.

In one study, the neural correlates of *semantic prediction generation* were described based on eye tracking and functional magnetic resonance imaging (Bonhage, Mueller, Friederici, & Fiebach, 2015). Participants read jabberwocky sentences, regular sentences and non-word lists up to the pre-final word. The final target word appeared with a temporal delay and its position on the screen depended on the word category (noun versus verb). The participants' anticipatory eye-movements into the target word-area were considered as an indication of their linguistic predictions. In addition, participants had to decide whether the target words were a plausible continuation of the word sequences. Specific subcortical activation linked to semantic predictions, achieved by contrasting the

Table 6
Overview of the subcortical activation patterns in the 12 studies in which the neural correlates of **semantic sentence comprehension** were reported.

References	Task content	Task condition	Subcortical activation	
			Hemisphere	Subcortical structures
a) Semantic violation processing (n = 6)				
McAvoy et al. (2016)	Passively listening to (im)plausible sentences	Implausible > plausible	R	Cerebellum (lateral inferior/posterior)
Moberget et al. (2014)	Reading (im)plausible sentences + plausibility judgment	Plausible > scrambled	R	Cerebellum (posterior)
			L/R	Caudate nucleus
			L/R	Putamen
		Implausible > plausible	L/R	Cerebellum (posterior)
Kuperberg et al. (2008)	Reading (im)plausible sentences + plausibility judgment	Animacy violations > morphosyntactic violations	R	Caudate nucleus
Ye et al. (2014)	Reading (im)plausible sentences	Implausible > plausible	L	Caudate nucleus
			R	Thalamus
Rothermich and Kotz (2013)	Listening to (im)plausible sentences + plausibility judgment	Implausible > plausible	-	-
Friederici et al. (2003)	Listening to (im)plausible sentences + plausibility judgment	Implausible > plausible	-	-
b) Semantic prediction (n = 1)				
Bonhage et al. (2015)	Predictive eye gaze reading task of (im) plausible sentences + plausibility judgment	Regular > jabberwocky	L/R	Cerebellum
			L/R	Thalamus
			L/R	Putamen
c) Ambiguity (n = 1)				
Mestres-Missé et al. (2014)	Reading (un)ambiguous sentences + plausibility judgment	Ambiguous > unambiguous	L/R	Anterior dorsomedial striatum
			L	Posterior dorsomedial striatum
		Subordinate > dominant	R	Anterior dorsomedial striatum
d) Metalinguistics (n = 4)				
Groussard et al. (2010)	Processing of proverbs	Proverbs > perceptual control condition	R	Cerebellum (posterior)
Bekinschtein et al. (2011)	Processing of humor	Jokes > non-jokes	L/R	Ventral striatum
Obert et al. (2016)	Processing of irony	Irony > literal	L	Caudate nucleus
Stringaris et al. (2007)	Processing of metaphors	Metaphoric > literal	L/R	Cerebellum
			L	Thalamus

activity pattern of the regular and jabberwocky condition[4] (regular > jabberwocky), included the *bilateral thalamus, putamen* and *cerebellum*. Interestingly, overall activation clusters were larger in the right hemisphere.

Semantic ambiguity processing was investigated in the study of Mestres-Missé, Bazin, Trampel, Turner, and Kotz (2014) by means of an orthographic semantic anomaly judgment task. Functional imaging revealed significantly larger activation for ambiguous compared to unambiguous sentences in the *bilateral anterior dorsomedial striatum (aDMS)* and the *left posterior DMS*.

Finally, 4 studies focused on *metalinguistic aspects* of sentence comprehension (Bekinschtein, Davis, Rodd, & Owen, 2011; Groussard et al., 2010; Obert et al., 2016; Stringaris, Medford, Giampietro, Brammer, & David, 2007). Groussard et al. (2010) investigated the neural correlates of proverb processing. Subjects listened to the beginning of a popular saying or proverb and had to decide whether the second part matched the first by means of a button response. PET scan analyses revealed the activation of the right posterior cerebellum. Bekinschtein et al. (2011) compared the activation when listening to jokes and non-jokes. The activity in the bilateral striatum was linked to the processing of humor. Similarly, processing ironic sentences revealed *left caudate* activation (Obert et al., 2016). Finally, in Stringaris et al. (2007), activation of the left thalamus was associated with deriving meaning from metaphoric sentences. Thus, the four studies on metalinguistic sentence comprehension revealed the main involvement of the *right posterior cerebellum* and the *left thalamus* and *caudate nucleus*.

4. Discussion

In this manuscript, we provided a systematic review and meta-analyses (ALE) of the subcortical involvement in verbal semantic comprehension both at word and at sentence level. As hypothesized, the results of this review indicate that the cerebellum, thalamus and caudate nucleus each contribute to semantic comprehension by fulfilling a specific cognitive function. However, these findings

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[4] **Regular sentences:** linguistic predictions are based on semantic and syntactic information. **Jabberwocky sentences:** sentences in which the grammatical structure is retained, but the content words are replaced with pronounceable non-words. Hence, linguistic predictions are exclusively based on syntactic information (word category).

should be interpreted with caution since the quality assignment revealed important methodological limitations in the included studies.

Quality of evidence – Three important limitations were detected by the study quality assessment. First, there was a limited use of a standardized test to assure normal cognition (word level: 17.9%, sentence level: 8.3%). No formal investigation of cognitive performance might have led to the inclusion of participants with mild cognitive impairments, in which brain alterations have been described (Granziera et al., 2015; Zhang et al., 2013). Second, only a minority of the included studies (word level: 23.1%, sentence level: 8.3%) reported the education level of the participants. This compromises generalizability of the reported findings, as there is no guarantee that the tested subjects are representative for the entire population. Third, fifteen studies at word level (33.3%) used a control task in which the phonological or orthographic demands were not comparable with those demands in the semantic task. Hence, the relative difference between the semantic and control task is likely to confound semantic with phonological or orthographic processes (Binder et al., 2009). When considering these limitations, results of future studies might slightly differ.

Cerebellum – Posterior cerebellar activity was reported both in studies on semantic word and sentence comprehension. This posteriorly situated activity can be attributed to the specific anatomy of the cerebellum. Connectivity analyses revealed the existence of separate cerebello-thalamo-cerebral loops for both sensorimotor and cognitive functions (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Habas et al., 2009). The cognitive loops, connecting the right posterior cerebellum (Buckner et al., 2011), the left thalamus and left cortical areas have been implicated to support several aspects of language processing (Stoodley & Schmahmann, 2010).

At word level, the results of the ALE-analysis of categorization tasks indicated two above-chance significant clusters located in the right posterior cerebellum, namely the right tuber (Lobule VIIB) and uvula (Lobule IX). The ALE-results support the hypothesis that the right posterior cerebellum is linked to executive functioning on the one hand and adequate decision-making on the other hand. This can be explained by the fact that in most of the categorization studies (13/14 - 93%) the neural correlates of rule-based categorization were described. Such tasks depend, besides semantic retrieval, on verbal working memory, selective attention and adequate decision-making. As the right posterior cerebellum projects to the left prefrontal and cingulate cortex (core structures in executive functioning ((Breukelaar et al., 2017; Niendam et al., 2012)), by way of a cerebello-thalamo-cortical network (Habas et al., 2009), it has been linked to several executive functions before, including verbal working memory (Chen & Desmond, 2005; Mariën et al., 2014; Marvel & Desmond, 2010) and selective attention (Le, Pardo, & Hu, 1998). Moreover, Broche-Pérez et al. demonstrated that the right cerebellum, the left thalamus and the left prefrontal and cingulate cortex are involved in adequate *decision-making* (Broche-Pérez, Jiménez, & Omar-Martínez, 2016). Studies investigating the neural correlates of synonym, ambiguity and reading tasks (not included in the meta-analysis) support the abovementioned cerebellar functions. More specifically, these results indicated that the higher the cognitive demands (e.g. synonym judgment of abstract versus sensory words, association of ambiguous versus unambiguous words), the greater the increase of posterior cerebellar activity (Bedny et al., 2008; McAvoy et al., 2016). As a result, the cerebello-thalamo-cortical network is supposed to be more active in difficult semantic conditions, requiring more executive functions. In this line, a reference can be made to verbal fluency deficits, the most frequently observed production impairments in individuals with cerebellar damage (Bellebaum & Daum, 2007). Performance on such fluency tasks relies on phonological and semantic retrieval, but also requires executive functions (Crawford, Parker, & McKinlay, 1992). Despite conflicting results on the laterality (left/right) and specificity (phonologic/semantic) of cerebellar involvement in verbal fluency, these findings support an executive cerebellar function (Mariën et al., 2014). Finally, the involvement of the cerebellum in reading tasks has been highlighted before in multiple studies (Fiez, 2016; Fulbright et al., 1999; Vlachos, Papathanasiou, & Andreou, 2007). Several cerebellar functions during silent reading have been described, namely inner speech (Ito, 2008), eye movements (Miall, Reckess, & Imamizu, 2001) and timing aspects (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002).

At sentence level, results revealed the involvement of the right posterior cerebellum in semantic prediction generation and evaluation. Prediction generation, more specifically using the context to predict the next word, was reported in one study (Bonhage et al., 2015). This feedforward linguistic control process can be linked to the hypothesis that the cerebellum supports the detection of patterns that allow a response to be predicted (Braitenberg, Heck, & Sultan, 1997; Molinari et al., 1997), such as the prediction of sensory events (Nixon, 2003). These findings were expanded to the verbal domain (Molinari et al., 2008), indicating a role of the posterior cerebellum in analyzing the incoming information in order to predict the upcoming information. Similarly, violations of these predictions (e.g. semantically implausible sentences) revealed more activity compared to semantically plausible sentences in the right (Moberget et al., 2014) or bilateral posterior cerebellum (McAvoy et al., 2016). These results suggest that the posterior cerebellum is not only involved in prediction generation, but also in the evaluation of predictions (feedback linguistic control). Together, generation and evaluation of predictions are two important aspects of internal models. Similar to the “Directions into Velocities of Articulators” model for speech production (Guenther, 2006), an internal model for comprehension has recently been described. Following Fiez (1996), who suggested that the cerebellum contributes in tasks that are initially effortful, but are performed more automatically with practice, Argyropoulos and colleagues hypothesized that the cerebellum forms internal models by storing associative memory traces of phonological, semantic and syntactic characteristics of words. These internal models would receive a copy of the linguistic input, processed at each stage by a fronto-temporal network, via the fronto-ponto-cerebellar circuit. Subsequently, a prediction of the upcoming information would be provided via the cerebello(dentate)-thalamo-prefrontal circuit. When a prediction violation occurs, this error signal would train the internal model for more accurate predictions in the future (Argyropoulos, 2009, 2016). Our results support the hypothesis of a right posterior cerebellar contribution in linguistic feedforward/-back control processes. Nevertheless, only limited research on semantic prediction generation and evaluation has been conducted in healthy individuals. Therefore, these findings are preliminary and need to be confirmed by future research.

Altogether, the results of this systematic review reveal a higher cognitive control function of the cerebellum in verbal semantic comprehension. This finding seems contradictory to results of Lesage, Nailer, and Miall (2016) who suggested that the right cerebellum (Crus II and cerebellar vermis) contributes in the early consolidation (acquisition and storage) of lexico-semantic associations. Their hypothesis was based on a short-term vocabulary learning task in which right cerebellar, and not cerebral, recruitment positively correlated with off-line performance after the experiment. Since this type of task was not examined in our included studies, we can neither confirm nor refute their hypothesis. However, these findings should be confirmed in future studies, including the examination of right cerebellar involvement in long-term lexico-semantic consolidation processes.

Caudate nucleus & thalamus – At word level, the co-occurring involvement of the left, right or bilateral caudate nucleus and thalamus in compositional association (ALE-analysis), noncompositional association (Assaf et al., 2006; Kraut et al., 2002b), ambiguity (Ketteler et al., 2008a, 2008b) and category-specific reading (González et al., 2006) tasks is a striking result. The contribution of bilateral or right subcortical nuclei might seem odd as we would expect a reliance on the language dominant left hemisphere in right-handed individuals (Knecht et al., 2000). Nonetheless, both clinical and functional imaging results are consistent with bilateral hemispheric contributions to semantic comprehension (Beeman et al., 1994; Gainotti, Caltagirone, Miceli, & Masullo, 1981; Hagoort, Brown, & Swaab, 1996; Rodd, Davis, & Johnsrude, 2005). Moreover, the right caudate ALE-cluster in compositional association may support anatomical findings in non-human primates, namely a projection of cortical fibers to either the ipsilateral or contralateral caudate nucleus or to both caudate nuclei (Fisher, Shiota, Levine, Hull, & Buchwald, 1984a; 1984b). However, in one of the studies contributing to the significant right caudate ALE-cluster (Seghier and Price, 2013), both ambidextral and left-handed individuals were included in addition to right-handed subjects. As revealed by Knecht et al. (2000), the incidence of right hemispheric language dominance is larger in ambidextrals and left-handed subjects (15% and 27% respectively), compared to right-handed people (4%). Hence, their inclusion might have influenced the results of the meta-analysis.

Interestingly, Stocco et al. (2010) reported that the role of the caudate nucleus (as part of the basal ganglia) is to “determine the state of cortical regions”. Such a modulation of cortical areas must be mediated through thalamic nuclei, relying on the anatomical cortico-striato-thalamo-cortical loops (Alexander et al., 1986; Jahanshahi et al., 2015; Murdoch, 2009). Within these loops, a distinction is made between a direct (cortico-striato-globus pallidus pars interna (GPi)-thalamo-cortical) and indirect (cortico-striato-globus pallidus pars externa (GPe)-nucleus subthalamicus (STN)-GPi-substantia nigra pars reticulata (SNr)-thalamo-cortical) pathway (Alexander et al., 1986), resulting in oppositional effects (excitation/inhibition) upon cortical areas. Regarding their anatomical connectivity, the co-occurring involvement of the caudate nucleus and thalamus in multiple semantic tasks is a plausible result. Our systematic review confirms an inherent collaboration between both subcortical structures in verbal semantic comprehension. This finding supports extended versions of the Selective Engagement model (Crosson, 1985; Nadeau & Crosson, 1997) in which the caudate nucleus and thalamus gate the semantic information flow by monitoring frontal and temporo-parietal activity (Kraut et al., 2003a, 2003b; Scimeca & Badre, 2012) and control the activation of an integrated concept (Hart et al., 2013). In the paragraphs below, we discuss the results of the functional imaging tasks that substantiate such a contribution in controlling the access (gating) and integration of semantic features.

A caudato-thalamic gating function is supported by results from compositional association, category-specific word reading and ambiguity tasks. The ALE-analysis of subcortical activation during compositional association revealed a left dorsomedial and right caudate activation cluster. Similarly, during the silent reading of odor- and taste-related words, activation of the left thalamus (Barrós-Loscertales et al., 2012; González et al., 2006) and the left caudate nucleus (González et al., 2006) was reported (in addition to the activation of a widely distributed cortical network of language-related areas and parts of the olfactory and gustatory system). In both tasks, access to the conceptual representations of one or more items is required in order to comprehend the words and to manipulate the information if necessary (e.g. searching for similarities). The semantic features of these concepts are represented in modality-specific cortical areas or “spokes”, namely the perception, action and affective systems of the brain (Binder & Desai, 2011; Garagnani & Pulvermüller, 2016; Pulvermüller & Fadiga, 2010). In terms of selective engagement, only the necessary semantic features and “spokes” need to be engaged, while disengaging the other. In this context, we propose that the caudate nucleus regulates the thalamic output, resulting in the (de)activation of cortical semantic areas. This gating process corresponds to the model of Kraut et al. (2003a, 2003b), proposing the dorsomedial nucleus as part of a semantic search circuit in conjunction with frontal areas, and to the model of Scimeca and Badre (2012), specifying the modulatory function of the caudate nucleus (Stocco et al., 2010) as “gating representations with a high utility in a specific context towards the prefrontal cortex”. In this context, verbal semantic comprehension disorders and semantic paraphasias in patients with thalamic lesions might be linked to an impaired gating function (De Witte et al., 2011; Llano, 2013).

Furthermore, caudato-thalamic gating might be attributed when words have multiple meanings, more specifically when enhancing one meaning and suppressing another. D. and S. Ketteler each reported a study in which the neural correlates of semantic ambiguity processes were investigated. The authors described an increase of left widespread thalamic (Ketteler et al., 2008a, 2008b) and bilateral caudate activity Ketteler et al., 2014) when the ambiguity of a homonym pair increased. The integration of both study results confirms the hypothesis of Chenery et al. (2008), namely a striato-thalamo-cortical circuit that is responsible for the enhancement and suppression of ambiguous word meanings. Relying on this hypothesis, accurate ambiguity resolution might be seen as a subcortical fine tuning process, emerging from the interplay between the thalamus and caudate nucleus (Ketteler et al., 2008a, 2008b). Further evidence for this hypothesis is provided by patients with a dominant thalamic lesion. Whelan, Murdoch, Theodoros, Silburn, and Hall (2002) described the negative impact of thalamotomies on the interpretation of ambiguous words.

A similar interaction between the caudate nucleus and thalamus was reported in noncompositional association tasks (SORT). The SORT-tasks can be considered as semantic fusion tasks, in which two stimuli (pictures or words) are both specific and sufficient features (e.g. desert and humps) in order to elicit a third object (camel). Functional imaging revealed left thalamic (Assaf et al., 2006; Kraut et al., 2002a, 2003) and right caudate activation (Assaf et al., 2006) when word-word pairs activated a third object, while bilateral caudato-thalamic activation was found for word-picture pairs (Kraut et al., 2002b). Thus, in addition to a gating function, the thalamus and caudate nucleus seem to support the integration/binding of semantic features, consistent with the function of the pre-SMA-caudato-thalamic circuit as proposed by Hart et al. (2013). Furthermore, Kraut et al. extended their previous results by estimating the time course of the fMRI activations. In this study, two different loci of signal changes in the thalamus were revealed, namely the dorsomedial and pulvinar nucleus. The slowest transients of the examined regions were shown by the pulvinar nucleus (Kraut et al., 2003a, 2003b). Based on these results, Kraut et al. described the function of the pulvinar thalamus as binding (cortically organized) semantic features by driving gamma rhythms (Kraut et al., 2003a, 2003b). However, these findings only partially correspond with the results of Slotnick, Moo, Kraut, Lesser, and Hart (2002). In their study, functional interactions between thalamic and cortical rhythms were demonstrated in a patient with bilaterally implanted thalamic electrodes. Again, the aspect of feature binding was linked to the thalamus, but the thalamic target for the electrodes was the dorsomedial nucleus. Future research is needed in order to unravel which specific nucleus/nuclei is/are involved.

Interestingly, the hypothesized contribution of the thalamus and the caudate nucleus in controlling the access (gating) and integration of semantic features can be applied to the results at sentence level as well. More specifically, bilateral thalamic activation was reported in the semantic prediction generation task (Bonhage et al., 2015), while right thalamic (Ye et al., 2014) and left, right or bilateral caudate activity (Kuperberg et al., 2008; Moberget et al., 2014; Ye et al., 2014) were revealed during the detection of violated semantic expectations. Analyzing the incoming information in order to predict and evaluate the upcoming information may depend on the selective engagement of cortical semantic networks, gated by the thalamus and caudate nucleus (Kraut et al., 2003a, 2003b; Crosson, 1985; Nadeau & Crosson, 1997). Feedback and feedforward semantic control have previously been linked to the cerebello-thalamo-frontal circuit (cfr. discussion part on the cerebellum) (Argyropoulos (2009); Ide and Chiang-shan (2011)). However, an additional contribution of the caudate nucleus in these processes would correspond to its role in the excitation of motor action schemas and the evaluation of action-outcomes (Danek, Öllinger, Fraps, Grothe, & Flanagin, 2015; Grahn, Parkinson, & Owen, 2008). A similar role in cognitive processes (such as semantic comprehension) might occur through functional coherence with the cerebellum, thalamus and frontal cortex (Allen et al., 2005). Nevertheless, this should be confirmed by future research.

Moreover, the left caudate activation reported during irony processing might be explained by the suggested role of the caudate nucleus in the enhancement and suppression of ambiguous word meanings (Chenery et al. (2008). Understanding verbal irony depends on the suppression of the meaning of what is being said, while enhancing the opposite of what is being said. Also, irony is often used because of its humorous effect (Roberts & Kreuz, 1994). Likewise, bilateral caudate activation was found in the study on humor processing (Bekinschtein et al., 2011). This finding could be assigned to the link between the striatum and reward processing (Chan, Chou, Chen, & Liang, 2012; Moran, Wig, Adams, Janata, & Kelley, 2004). As humor can be seen as a positive reward experience, caudate involvement is plausible.

Finally, the left thalamus appeared to be involved in deriving meaning from metaphoric sentences (Stringaris et al., 2007). In general, metaphors are defined as a semantic change, based on a similarity in form or function between the original concept named by a word, and the target concept named by this word (Grzega, 2004). Hence, the interpretation of these sentences relies on processes similar to the processes required in noncompositional association tasks (SORT). For example, the interpretation of the metaphor “time is money” relies on the identification of a third concept, which reflects features of both the concepts “time” and “money”, for example “working”. Thus, these findings provide additional evidence for the role of the left thalamus in semantic feature binding (Stringaris et al., 2007).

Remaining nuclei – The reporting of putaminal (reading, synonym judgment, semantic prediction generation), pallidal (reading), and subthalamic activation (synonym judgment) was scarce and difficult to interpret (Barrós-Loscertales et al., 2012; Bonhage et al., 2015; Carota et al., 2012; González et al., 2006). Hence, a clear function of these nuclei in verbal semantic comprehension cannot be formulated based on functional imaging studies in healthy individuals.

Nevertheless, the anatomic connection between the left anterior putamen and pars triangularis (Ford et al., 2013), a region linked to semantic processing (Friederici, 2002), suggests a specific function of the putamen. Based on the results of a recent meta-analysis (Viñas-Guasch & Wu, 2017), the left anterior putamen is associated with semantic retrieval and comprehension. The right anterior putamen showed co-activation with the left putamen and might therefore support certain semantic operations. However, the experiments included in this meta-analysis are characterized by a large variability in task demands (e.g. lexical decision versus verb generation). Thus, these results should be interpreted with caution. Furthermore, indications of a role of the globus pallidus and subthalamic nucleus (STN) in semantic processing mainly stem from verbal fluency studies. Semantic fluency decrements, especially alterations in switching between sub-categories, have been reported in pallidal and subthalamic surgery studies (Anzak et al., 2011; Saint-Cyr, Trépanier, Kumar, Lozano, & Lang, 2000; Tröster, Woods, Fields, Hanisch, & Beatty, 2002). Since both nuclei are connected with the fronto-striatal network (Murdoch, 2009), a network associated with verbal fluency (Baldo, Shimamura, Delis, Kramer, & Kaplan, 2001), these nuclei might support this process. However, Wahl et al. (2008) reported no involvement of the globus pallidus internus and the STN in semantic processing at sentence level, based on EEG-recordings of semantic language violations in DBS-patients.

Summarized, the specific role of the putamen, globus pallidus and STN in verbal semantic comprehension remains elusive. More research yielding spatial and temporal information is needed to provide insights into their contributions.

5. Conclusion

This systematic review and meta-analysis provide an overview of the current knowledge on the involvement of subcortical grey matter structures in verbal semantic comprehension. Results of the functional imaging studies in healthy participants revealed a contribution of the cerebellum, thalamus and caudate nucleus. At word level, the right posterior cerebellum might be linked to a semantic executive system required for effortful and strategic retrieval of semantic information and may be involved in adequate decision-making. The left thalamus, regulated by the caudate nucleus, might function as a subcortical hub, controlling the access and integration of cortically organized semantic features. Furthermore, the involvement of the cerebellum, thalamus and caudate nucleus in a semantic prediction generation and evaluation process at sentence level is preliminarily suggested. Nevertheless, more temporo-spatial research is needed to confirm our findings and to gain insights into the role of the putamen, globus pallidus and subthalamic nucleus in verbal semantic comprehension. Future research should take into account the important limitations that were revealed by the study quality assignment.

Conflicts of interest

None known.

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APPENDIX 1. SEARCH STRATEGY

Pubmed (via PubMed interface)

1. Semantics [Mesh] OR semantic*[TIAB]
2. Basal Ganglia [Mesh] OR "basal ganglia" [TIAB] OR "neostriatum" [TIAB] OR "lentiform nucleus" [TIAB] OR "lentiform nuclei" [TIAB] OR "lenticular nucleus" [TIAB] OR "lenticular nuclei" [TIAB] OR "Pedunculopontine Tegmental Nucleus" [Mesh] OR "pedunculopontine tegmental nucleus" [TIAB] OR "pedunculopontine tegmental nuclei" [TIAB] OR "pedunculopontine nucleus" [TIAB] OR "pedunculopontine nuclei" [TIAB] OR "Subthalamic Nucleus" [Mesh] OR "subthalamic nucleus" [TIAB] OR "subthalamic nuclei" [TIAB] OR "Substantia Nigra" [Mesh] OR "substantia nigra" [TIAB] OR "Thalamus" [Mesh] OR thalam* [TIAB] OR "globus pallidus" [TIAB] OR putamen [TIAB] OR "caudate nucleus" [TIAB] OR "caudate nuclei" [TIAB] OR "Cerebellum" [Mesh] OR cerebell* [TIAB] OR subcort* [TIAB] OR striat* [TIAB] OR corticostriat* [TIAB] OR corticosubcort* [TIAB]
3. 1-2 AND

Cochrane Central Register of Controlled Trials (CENTRAL)

1. [mh “Semantics”] OR (semantic*):ti,ab,kw
2. [mh “Basal Ganglia”] OR ("basal ganglia"):ti,ab,kw OR ("neostriatum"):ti,ab,kw OR ("lentiform nucleus"):ti,ab,kw OR ("lentiform nuclei"):ti,ab,kw OR ("lenticular nucleus"):ti,ab,kw OR ("lenticular nuclei"):ti,ab,kw OR [mh "Pedunculopontine Tegmental Nucleus"] OR ("pedunculopontine tegmental nucleus"):ti,ab,kw OR ("pedunculopontine tegmental nuclei"):ti,ab,kw OR ("pedunculopontine nucleus"):ti,ab,kw OR ("pedunculopontine nuclei"):ti,ab,kw OR [mh "Subthalamic Nucleus"] OR ("subthalamic nucleus"):ti,ab,kw OR ("subthalamic nuclei"):ti,ab,kw OR [mh "Substantia Nigra"] OR ("substantia nigra"):ti,ab,kw OR [mh "Thalamus"] OR (thalam*):ti,ab,kw OR ("globus pallidus"):ti,ab,kw OR (putamen):ti,ab,kw OR (“caudate nucleus”):ti,ab,kw OR ("caudate nuclei"):ti,ab,kw OR [mh “Cerebellum"] OR (cerebell*):ti,ab,kw OR (subcort*):ti,ab,kw OR (striat*):ti,ab,kw OR (corticostriat*):ti,ab,kw OR (corticosubcort*):ti,ab,kw
3. 1-2 AND

Web of Science

1. TS = (semantic*)
2. TS = (“basal ganglia”) OR TS = (“neostriatum”) OR TS = (“lentiform nucleus”) OR TS = (“lentiform nuclei”) OR TS = (“lenticular nucleus”) OR TS = (“lenticular nuclei”) OR TS = (“pedunculopontine tegmental nucleus”) OR TS = (“pedunculopontine tegmental nuclei”) OR TS = (“pedunculopontine nucleus”) OR TS = (“pedunculopontine nuclei”) OR TS = (“subthalamic nucleus”) OR TS = (“subthalamic nuclei”) OR TS = (“substantia nigra”) OR TS = (thalam*) OR TS = (“globus pallidus”) OR TS = (“putamen”) OR TS = (“caudate nucleus”) OR TS = (“caudate nuclei”) OR TS = (cerebell*) OR TS = (subcort*) OR TS = (striat*) OR TS = (corticostriat*) OR TS = (corticosubcort*)
3. 1-2 AND

Embase (via Embase.com interface)

1. ‘Semantics’/de OR semantic*:ab,ti
2. ‘Basal Ganglion’/exp OR ‘basal gangli*’:ab,ti OR ‘neostriatum’:ab,ti OR ‘lentiform nucleus’:ab,ti OR ‘lentiform nuclei’:ab,ti OR

‘lenticular nucleus’:ab,ti OR ‘lenticular nuclei’:ab,ti OR ‘Pedunculopontine Tegmental Nucleus’/de OR ‘pedunculopontine tegmental nucleus’:ab,ti OR ‘pedunculopontine tegmental nuclei’:ab,ti OR ‘pedunculopontine nucleus’:ab,ti OR ‘pedunculopontine nuclei’:ab,ti OR ‘subthalamic nucleus’:ab,ti OR ‘subthalamic nuclei’:ab,ti OR ‘substantia nigra’:ab,ti OR ‘Thalamus Nucleus’/exp OR thalam*:ab,ti OR ‘globus pallidus’:ab,ti OR ‘putamen’:ab,ti OR ′caudate nucleus':ab,ti OR ‘caudate nuclei’:ab,ti OR ‘Cerebellum’/exp OR cerebell*:ab,ti OR subcort*:ab,ti OR striat*:ab,ti OR corticostriat*:ab,ti OR corticosubcort*:ab,ti

3. 1-2 AND

APPENDIX 2. QUALITY LABEL - Detailed terms and weighted distribution of points

INTRODUCTION	**/1**
1) Was the research question or objective clearly stated?	/1
METHOD (PARTICIPANTS-TASK-IMAGING TECHNIQUE-STATISTICS)	**/11**
PARTICIPANTS	
2) Was the study population clearly specified and defined?	/1
● Sex (distribution) + age (mean, SD)	/1
● Right-handedness	/1
● Normal cognition (explicitly tested)	/1
● Education years (mean, SD) + language	
3) Was the participation rate of eligible persons at least 50%?	/1
4) Were the exposure measures clearly defined, valid, reliable and implemented consistently across all study participants?	
TASK	
● Is there a clear description and argumentation of the task used during neuroimaging?	/1
● Is there a clear description of the test procedure?	/1
● Is there a clear description of the used materials?	/1
● Is a control task used with comparable phonological, orthographical, (morpho)syntactic and prosodic demands as in the semantic task?	/1
IMAGING	
● Is there a clear description of the imaging acquisition?	/1
STATISTICS	
6) Is there a clear description and argumentation of the statistical analysis?	/1
RESULTS	**/2**
7) Were the outcome measures (neuroimaging results) clearly defined, valid and reliable?	/2
DISCUSSION	**/1**
8) Were limitations/suggestions for further research described?	/1
TOTAL	**/15**

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